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# ON THE SHELL OF LITTORINA LITOREA AS MATERIAL FOR THE STUDY OF VARIATION.

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THE common periwinkle, *Littorina litorea*, seems at first especially suitable for a statistical study of the effect of a new environment upon type and variability. For the best evidence, according to Morse ('80) and Ganong ('86), goes to show that this species has been introduced from Europe into Nova Scotia and New England within the last fifty years. It was first reported from Halifax by John Willis in 1857. Previous to this date no mention is found of the species in any list of the shells of Nova Scotia, New England, or the Gulf of St. Lawrence. Furthermore the shell is not found fossil in these regions, and is not found in the prehistoric shell heaps. The species seems therefore to have been introduced into America somewhere about the middle of the nineteenth century.

After its introduction it spread gradually southward along the coast of New England as far as Long Island Sound. In every place where it has appeared north of Cape Cod it has increased enormously and in many cases nearly driven out the indigenous species of Littorina, until it is now probably the most abundant gasteropod on the coast. But south of the Cape it is only fairly abundant in certain stations.

Thus we have in *L. litorea* a species which has been introduced into a new environment within a comparatively short time. One might expect *a priori* that this species on migrating into a new area would find new conditions and be subjected to new factors of natural selection, which would tend to establish a new type, or else that the species, having escaped, perhaps, from some of the checks that limited its variability in its former environment, might show a greater range of variation under the new conditions. By a statistical study of *L. litorea* one might hope to determine whether one or both of these suppositions are true, and whether evolution is taking place in this introduced species. These results, if trustworthy, would be of very considerable value at this time, because the number of quantitative determinations of the present rate of evolution that have been made heretofore are very few indeed, and students of the subject are seeking to accumulate sufficient data to remove the theory of evolution from the realm of inference to that of observed fact.

It was for this reason that the authors planned a statistical study of *L. litorea*. We proposed to compare variability and type in two generations of shells which had been subjected to their environments for different lengths of time. We hoped to find material for this purpose in measurements of some character in young shells and of the same character in the upper part of fully grown specimens, as Weldon ('01) had done in his study of Clausilia.

Thus by comparing the type and variation of the same character in the present young shells and in the survivors of a former generation of young shells we might expect to discover any selection that may be taking place with respect to that character and to determine whether the result is progressive evolution or is simply periodic, *provided of course, that the character chosen is known to remain constant during the life of the individual.* The only available character to measure seemed to be the angle at the apex of the shell.

For this investigation a large number of living specimens of all sizes were collected at Winthrop, Mass., from spaces between the rocks at low tide, during the month of February, 1902.

Many of the oldest shells were plainly much eroded at the apex and unfit for our purpose. But all of the smaller shells and many of the large ones appeared to be in good condition. It was noticeable, however, that the larger shells were generally less acute at the apex than the very small ones. The suspicion that this fact aroused was further increased by examination with the hand lens, which showed that near the apex of all the shells the surface was roughened with fine depressions like minute pinholes. Evidently some process of erosion was at work, and it would be useless to proceed with our investigation unless it could be shown that the amount of erosion was so slight as to be negligible. It occurred to us that possibly the amount of erosion, on the contrary, might be even greater than would be indicated by the condition of the surface. If the loss of material from the surface should be balanced by the deposition of new shell within the cavity, this might mask the erosion to such an extent as to make it impossible to determine from the appearance of the surface whether any given shell was much or little eroded. With such an uncertainty any results obtained by the comparison of the apexes of old shells with those of young ones would be utterly worthless.

We proceeded, therefore, to determine the amount of erosion in shells of various sizes from the smallest to the largest. The method employed was the study of thin sections made through the apex of the shell in the plane of the columella.

The sections were made in the following manner: — The soft parts having been removed, the rounded part of the shell was first ground from each side on an ordinary grind-stone used for the sharpening of instruments. A slice was thus obtained through the middle of the shell. One side of this was ground with emery on a grinding machine used for making sections of minerals[1] until a surface passing through the middle of the columella was obtained. This surface was made perfectly even by polishing with a paste of diatomaceous earth on a ground glass plate. The polished side was then cemented to a glass plate with Canada balsam, after which the other side was ground down and polished in the same way until the section was sufficiently thin. The section was then cleaned and mounted in Canada balsam in the usual manner under a cover glass.

In this way about a dozen slides were made. Figs. 1, 2, 3, and 4 are camera lucida drawings of sections of four shells of different sizes. Thus we have sections of two young shells, Figs. 1 and 2, a shell which is not quite fully grown, Fig. 3, and one of full size, Fig. 4. The openings in Fig. 1 are numbered, beginning at the top, and the corresponding openings in the other sections are given the same numbers. Of course, the holes in any two sections will not correspond exactly, as the planes of the sections are not made accurately at the same angular distance from the origin of the spiral, but it can easily be seen which holes are of about the same size. These openings are, of course, the places where the lumen of the shell lies in the plane of the section and serve as a convenient index of erosion. In each of the older shells we can see the outline of the younger stages. The line *a–b* in each section represents the lower boundary of the stage corresponding to Fig. 1.

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[1] The authors are much indebted to Dr. C. H. Warren for helpful suggestions and assistance in using this machine.

The shell represented by Fig. 1 is about 3 mm. long and 2.5 mm. broad, and is the smallest one that we were able to cut. On the body-whorl were three or four ribs somewhat darker in color than the rest of the shell. This marking extended into the next whorl, but toward the apex of the acute spire the shell was smooth. In the section the lumen of the shell is cut distinctly eight times, leaving eight openings in the section, and at the apex there is an indication of another half turn of the spiral. Each half turn of the spiral, or opening in the section, is numbered consecutively, beginning at the apex.

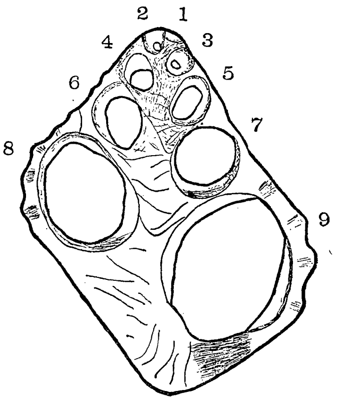

Fig. 1. Camera drawing of a median longitudinal section of a young shell. × 16.

Microscopic examination of the section, Fig. 1, shows that the main part of the shell is composed of a translucent material of a pearly white color with fine darker lines of growth or fracture lying at more or less acute angles to the sides of the lumen. This material may be called the *primary shell.* Under the ribs it is stained a dark yellowish brown color for nearly its whole thickness, and in the upper part of the shell the whole columella is colored. Around each opening of the section the boundary of the primary shell is clearly defined by a very fine but perfectly distinct dark line. Within this boundary the lumen of the shell is more or less completely lined by a layer of pearly material that we may call *secondary shell.* This may be white and clear or it may show a yellowish stain or fine lines of growth parallel to the surface of the lumen. The secondary shell has evidently been deposited after the formation of the primary shell, and there is a considerable amount of it, even in this very young specimen. In the upper part of the spire the secondary has nearly filled the original cavity of the primary shell, so that openings 2 and 3 are almost obliterated, and No. 1 is quite so. Moreover the lumen at openings 2 to 4 is eccentric, the thickest part of the secondary shell being on the outer side. It will be noticed, also, that the outlines of the primary lumen at openings 1, 2, and 3 are incomplete, being cut by the outer surface of the shell. Evidently erosion has been at work already to such an extent as to have removed the whole thickness of the original outer wall of the first whorl, and, if no secondary shell had been secreted, there would be an opening from the cavity to the exterior at this place.

Fig. 2 represents a similar section of a shell about half again as large as Fig. 1, that is, 5 by 4.5 mm. The specimen is in good condition with well marked dark ribs upon the body-whorl, and with an acute apex, but the apical angle is greater than in Fig. 1.

Assuming that Fig. 2, has passed through a stage corresponding to Fig. 1, a comparison of the size of the opening indicates that the increased size has been attained by the addition of another whorl. But the total number of whorls in the two shells remains the same. This paradoxical condition may be explained by supposing the first whorl, openings 1 and 2, to have entirely disappeared as the result of erosion. That this is the true explanation is rendered highly probable by microscopic examination of the section. In the first place, the primary outlines of openings numbered 5 to 9 agree in their dimensions very closely with the correspondingly numbered openings of Fig. 1; and in the second place, the evidences of erosion are abundant. Within the primary shell between openings 9 and 11 there is a fine wavy black line (*b*) that was evidently at the surface of the body whorl during the stage of Fig. 1. The distance between this line and the primary outline of opening 9 is greater than the distance between this outline and the present outer surface of the whorl. The difference between these two distances gives a measure of the amount of erosion that has taken place since the time when the wavy line was covered by the present body whorl. Similar wavy lines are seen below openings 8 and 7 and there the differences are greater, showing an increased amount of erosion toward the apex, and the loss by erosion is still greater at openings 6 and 5 where the secondary shell is exposed at the surface.

The same thing is shown more clearly in Fig. 3, a normal, nearly full grown shell about 15 mm. long. Between openings 11 and 13 there is a wavy line that forms a continuous curve with the surface of the shell at 11. Here the erosion has proceeded only so far as to smooth off the ribs, while below openings 10 and 9 the wavy lines end abruptly almost at right angles to the surface, and the exposed secondary shell at these openings furnishes further evidence of erosion. At opening 9 the secondary shell itself is entirely removed on the outer side. But the lumen of the shell is prevented from opening to the exterior by a thick layer of *tertiary shell*, which has been deposited within

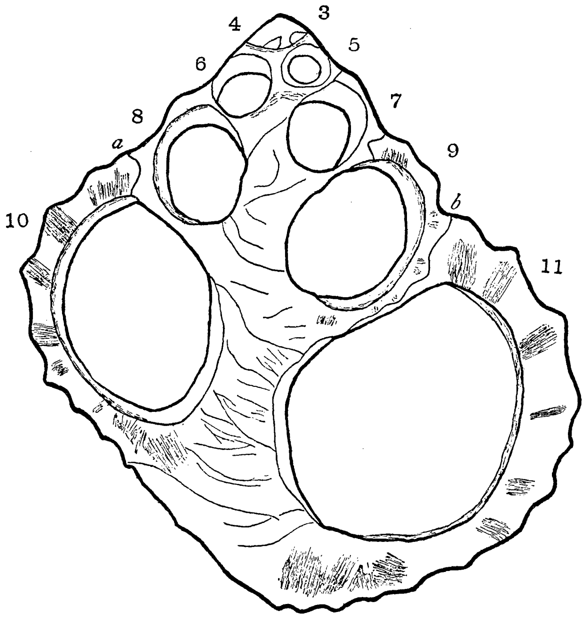

Fig. 2. Similar section of a somewhat larger shell. × 16.

the secondary and exhibits lines of growth parallel to its own surface and unconformable with those of the secondary shell. All of the openings above 13 in this specimen show a layer of tertiary shell, which becomes progressively thicker toward the apex. The numbers assigned to the openings in this specimen are obtained by comparison with Fig. 2, and, if the reasoning applied to that figure will hold for this one, the first five openings, that is two whorls and a half, have disappeared entirely.

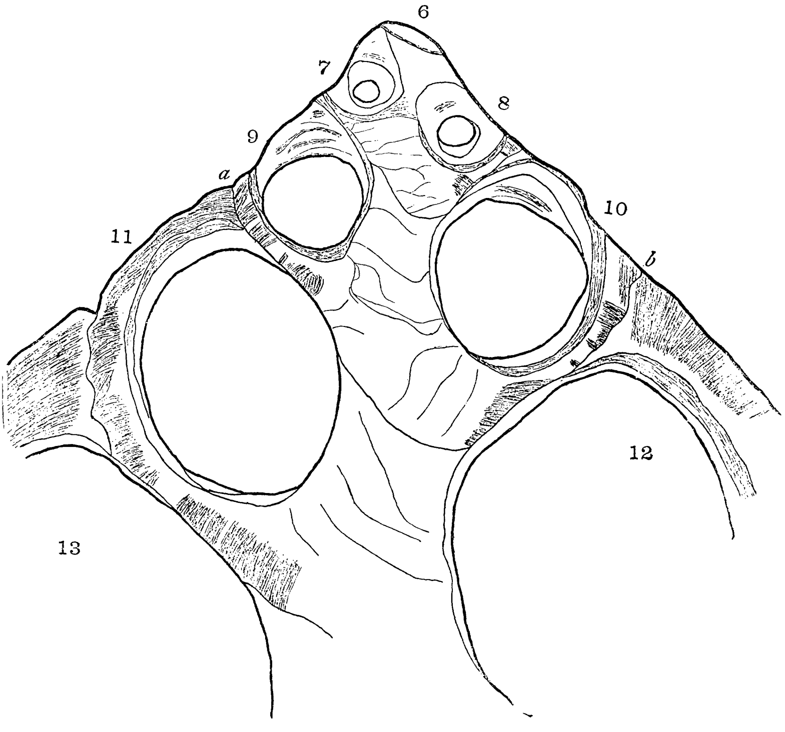

Fig. 3. Section of a nearly full-grown shell in good condition. The lumen is cut ten times but only seven of the openings are shown in the drawing. × 16.

Fig. 4 is from one of the largest of the specimens collected, about 20 mm. long. But somewhat larger shells are not rare. To the naked eye the rounded apex and white color of the apical region in this specimen indicated a considerable but not excessive amount of erosion. The difference in color is shown by the section to be due to the exposure of a large amount of tertiary shell, which is colored only in the inner layers. Comparison of this section with Fig. 2 indicates that the two upper whorls of this specimen contain openings 8, 9, 10, and 11, as shown in Fig. 6. The uppermost whorl has almost disappeared and the second one has lost the entire outer wall of both primary and secondary shell. So that of the shell formed during the stage of Fig. 2 there remains in this specimen only the columella of the two lower whorls and a portion of the lip region. While of the stage of Fig. 1 there remains only the merest fragment of the body-whorl (Fig. 5).

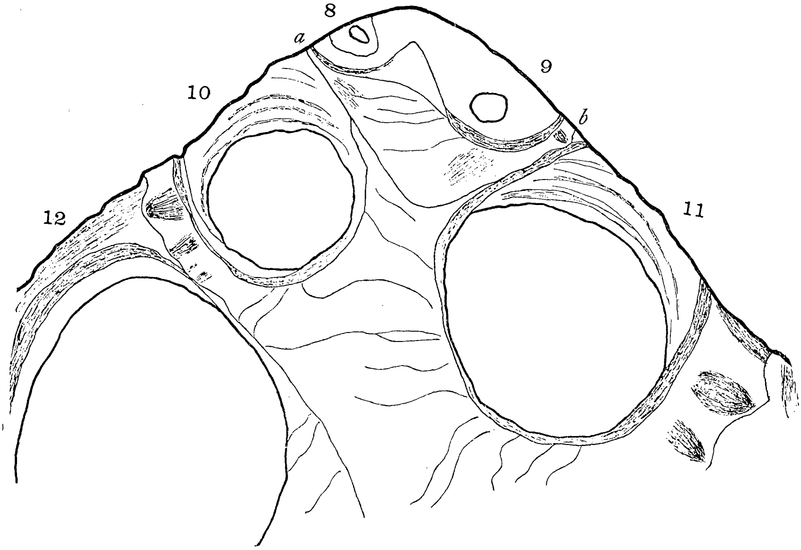

Fig. 4. Camera drawing of the upper part of a section through a shell about 17 by 17 mm. In the whole section the lumen is cut only nine times. × 16.

The actual shortening of the shell and the changes in shape due to erosion cannot be measured directly. But we can estimate them by comparing sections of younger and older stages, as in Figs. 5 and 6. By this method it is estimated that between the stages of Figs. 1 and 2 there has been a shortening of about 0.25 mm. In Fig. 3 this has increased to 0.6 mm. and in Fig. 4 to 1.4 mm. Or considering Fig. 1 as the initial stage of all the larger shells, the length of that portion of the shell has been reduced in the three subsequent stages by 8.3%, 20.0%, and

46.7% respectively. This amounts to a reduction in the total length of the shell at each stage of 5%; 4% and 7% respectively.

Assuming that, if there were no erosion, the outline of the section at the stage of Fig. 4 would be represented approximately by the combined continuous and dotted outlines in Fig. 5, it is evident that there has been a considerable increase in the magnitude of the apical angle. This would be shown still better by combining Figs. 1 and 6. The difference between the angles of Fig. 1 and Fig. 4 is 18°, or 19% of the apical angle of Fig. 4.

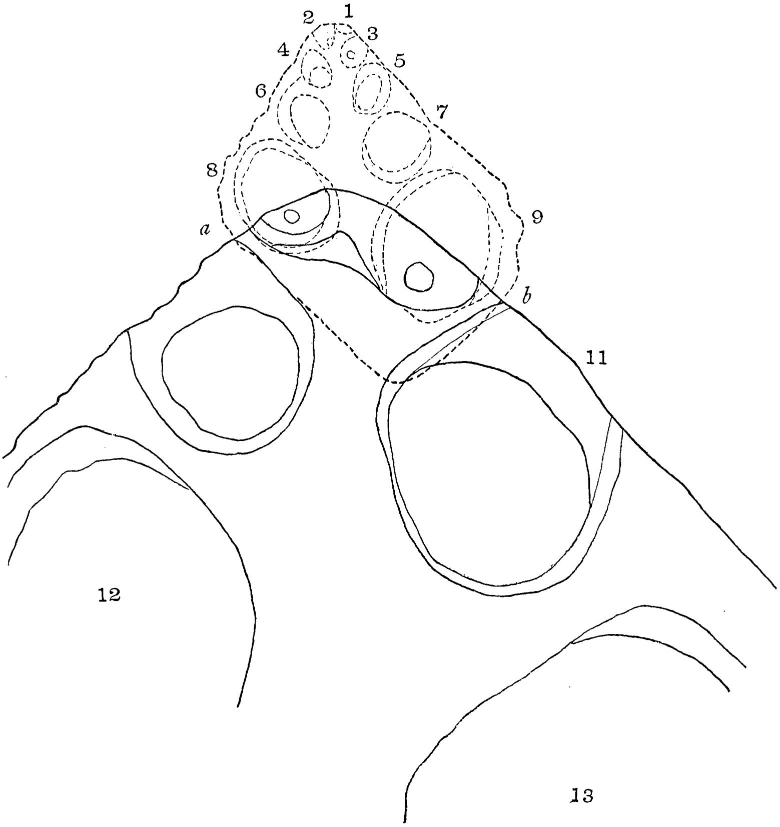

Fig. 5. Outline of Fig. 1 placed on Fig. 4 so that the corresponding openings coincide.

The loss of height in the shell of Fig. 4 is estimated at about 7%, while there is no evidence of any corresponding decrease in the breadth of the body-whorl. So the ratio of breadth to length, or the *ventricosity* of the shell, is a ratio of a slightly modified to a much modified character. The actual length of the shell in Fig. 4 is about 20 mm., its breadth, 17 mm., giving a ratio of 85%. But without erosion the length is estimated to have been 21.4 mm. giving a ratio of 79%. Thus the shell is now more ventricose by 6 degrees. In Fig. 3 the length is 15 mm., breadth, 13 mm., ratio, 87%; but the length without erosion would be about 15.6 mm. and the ratio would be about 83 %, an increase of ventricosity of 4 degrees.

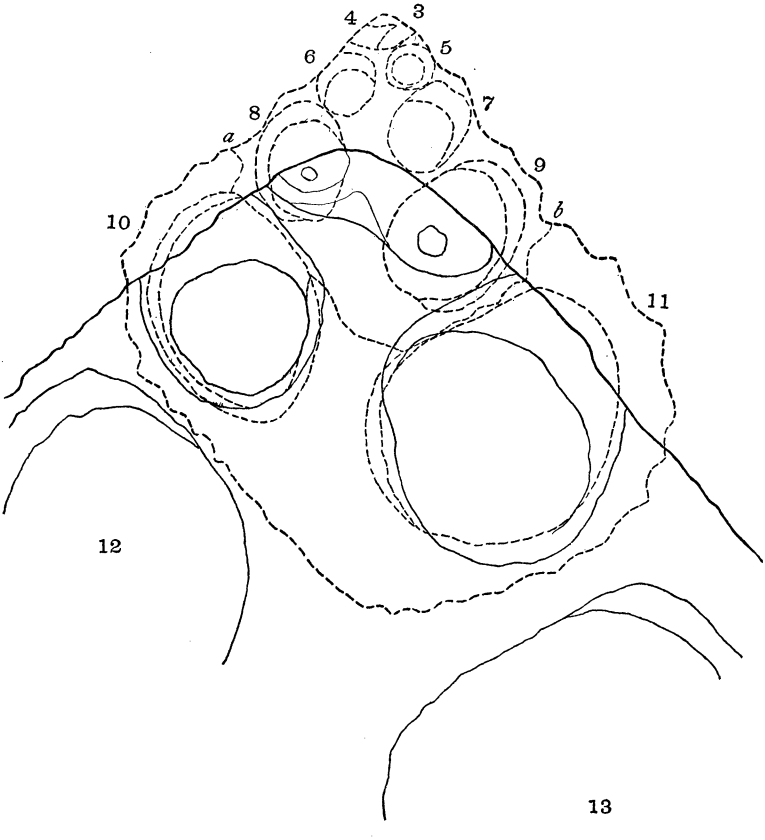

Fig. 6. Outline of Fig. 2 placed on Fig. 4 so that corresponding openings coincide.

Thus within the limits of our studies we find that in all stages of the growth of the shell of *L. litorea* there has been a change in both size and shape resulting from erosion. While the absolute amounts of these changes seem small, they are relatively large enough to falsify any comparisons that may be made between the variabilities and types at different localities or at different ages, unless a correction for erosion can be applied.

For our measurements would show, not the normal variability of growth, but the combined effect of variability of growth, variability in power of resistances to erosive agents, and perhaps variability of these agents themselves. To obtain data for the correction of our results would involve an investigation of the rate of erosion that would be too laborious to be undertaken.

Our attention was drawn to this species especially by the very interesting work of Bumpus ('98), who made a comparison of the variability and types in shells from three English localities with shells from ten stations on the New England coast. He concluded that in all the characters studied the shells from all the American localities (that is, those in the comparatively new environment) were more variable than those from any of the English localities. And he stated also that the American type is "more enlongated,[1] lighter in weight, more bulky, and the color markings are less pronounced."

His tests of variability were: — (1) Ratio of breadth and length, (2) Comparison of the extremes of this ratio, (3) Comparison of curves for different ages, (4) Weight, (5) Bulk, and (6) Color. Our results show that the first five of these tests of variability are rendered of doubtful value by the erosion. Or at any rate, the factor of erosion must be taken into account in the discussion of these results, for, as has been shown, the ratio of breadth to height is very considerably affected by the loss in height, the difference is the ratios amounting to as much as .05 or .06; while the total range of variation found by Bumpus was .17 in the British and .24 in the American series. And the difference between the means of the two series was only .014, much less than the probable effect of erosion in an apparently normal shell such as is represented in Fig. 3.

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[1] This evidently an error, for the average of the English mean ratios of breadth to height is 89.6 and the average of the American mean is 91. That is the American type is more ventricose.

It is in a comparison of ratios in shells of different ages, such as Bumpus made, that the effect of erosion would be most seriously felt. He found an increase of ventricosity in six localities and a decrease in seven. Doubtless the former would have been very much diminished and the latter augmented in the absence of erosion.

Weight and bulk are also affected by the combination of erosion without and deposition within. Color is the only remaining test, and that is rather an unsatisfactory measure of variability in this species.

Various explanations have been offered to account for the erosion of molluscan shells, which according to Cook ('95) is much more common among fresh-water forms than in those inhabiting the sea. Many years ago Lewis ('59) pointed out that the shells in a stream near Mohawk, N. Y., below the point where alkaline wastes were discharged into the water were much eroded, while above the point of pollution they were quite healthy and free from defect. Jeffries ('65) quotes the suggestion of J. R. Grove that the patches and irregular hollows on the surface of *L. litorea* may be due to electrolytic action arising from lack of homogeneity in the shell substance. Schrubsole ('86) found that certain English fresh waters containing from one half to four grains of lime per gallon had a strong erosive action on shells, while no such action was noticed in water containing eight and one third grains.

That filamentous plants penetrate many shells of molluscs and brachiopods, as well as numerous corals and other forms, was pointed out by Kölliker ('59). Later Bornet and Flahault ('89) summarizing the results of previous observers, described and figured eight genera of algæ and two fungi having the shell-boring habit, and they pointed out that these plants play an important part in the destruction of shells, especially in quiet waters. Recently, Duerden ('02) has drawn attention to the action of algæ in the disintegration of corals in the West Indies. We have not been able to discover however, any evidence of the presence of algæ or other plants upon the shells of Littorina collected during the winter months, and have no explanation to offer as to the cause of the erosion that we have observed.

This is, nevertheless, so great that we are reluctantly forced to the conclusion that *Littorina litorea*, which on account of its comparatively recent migration to our shores, and its great abundance and variability seemed an especially favorable object for statistical study, is after all not suitable for this purpose. In order to use this material we must either assume that the causes of erosion have a uniform intensity for all individuals, or else we must devise some easy method for determining the actual loss of substance in each individual. But even these precautions would not enable one to use this material for the solution of the special problem that we had in view.

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